

New Genera and Species of Ultrapsammophilous Namib Desert Lepismatidae (Thysanura)

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INTRODUCTION

Irish (1986b) described three species of Lepismatidae from the Namib dunes, which he referred to *Mormisma* Silvestri. He noted the biogeographical problems posed by the presence of species of the same highly apomorphic genus in two areas as far apart and as unrelated as the Namib and Sahara deserts. The study of the further ultrapsammophilous taxa which are described here has again highlighted this problem. In an effort to solve it, various characters which could not be studied before for lack of proper equipment at the time, were investigated. Most important among the latter were the antennal sensillae, the setation of the head capsule and the morphology of the pretarsal claws. Mendes (1982) first discovered the phylogenetic importance of the latter structures.

Watson & Irish (in press) report on the ecology of the species treated here.

The following institutional abbreviations were used:
CZ — Centro de Zoologia, I.I.C.T., Lisbon, PORTUGAL
SMWN — State Museum, Windhoek, SOUTH WEST AFRICA
TM — Transvaal Museum, Pretoria, SOUTH AFRICA

SYSTEMATICS

NAMIBMORMISMA Irish gen. nov.

Mormisma Silvestri, 1938 *sensu* Irish, 1986b (*pro parte*).

Type-species: *Mormisma muricaudata* Irish, 1986.

Body length up to 9 mm. Body shape squat. Hypodermal pigment absent. Macrosetae smooth. Antennal sensillae poculiform (Plate 1). (All reference to antennal sensillae in Irish (1986b) should be rejected as erroneous). Setation of head as in Figure 1. Distal segment of labial palp with three sensory papillae. Thoracic nota with wide marginal setal fringes. No trichobothrial areas. Urotergites I-VIII with 1+1 lateral setal fringes each, which are differentiated into 3+3 setal groups on the anterior urotergites. Urotergite IX

ABSTRACT

Sabulepisma multiformis gen. et sp. nov. and *Swalepisma mirabilis* gen. et sp. nov. (Thysanura: Lepismatidae) are described from the Namib Desert sand dunes, and *Namibmormisma* gen. nov. is proposed for some Namib species previously referred to *Mormisma* Silvestri. The probable phylogeny of these taxa is discussed.

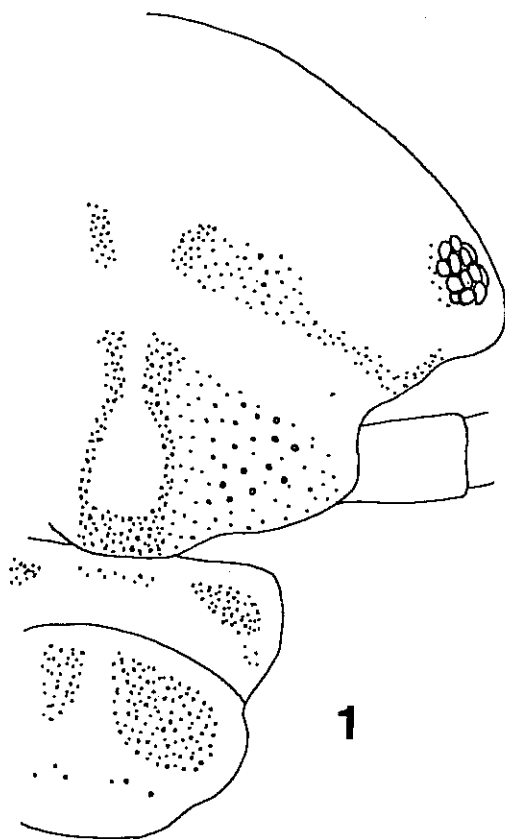


FIGURE 1: *Namibmormisma setosa*. Setation of head.

unsetated or with 1+1 setal groups. Urotergite X trapezoidal, short, with 1+1 lateral setal fields. Tarsal claws elongate, straight, one longer than the other (Plate 2), lacking empodia. Urosternites I and II with a median or a pair of median bristlecombs. Urosternites III-VII (female) or VIII (male) with 1+1+1 bristlecombs. Styli completely absent. Ovipositor very short, conical, apices of posterior gonapophyses unsclerotised. Parameres lacking.

Distribution: Namib Desert.

Etymology: a compound of "Namib" and *Mormisma* Silvestri; gender feminine.

The new genus *Namibmormisma* includes two of the three *Mormisma* species described by Irish (1986b), viz. *Namibmormisma muricaudata* **comb. nov.** and *Namibmormisma setosa* **comb. nov.** As will be shown in the discussion below, these species originated in the Namib Desert and are not directly related to the Saharan *Mormisma peyerimhoffi* Silvestri. We believe that classification should mirror phylogeny, and therefore propose a new generic name for these two Namib species, restricting *Mormisma* Silvestri to the type-species *M. peyerimhoffi* only. *Namibmormisma* is remarkably close to *Mormisma*, a fact ascribed to parallel evolution due to the similar microhabitats (dune hummocks) occupied by both genera. *Namibmormisma* differs from *Mormisma* as follows: *Namibmormisma*

has no styli, it has a median setal group on urosternite VII, and it has a differently setated head, lacking in particular the three setal tufts on the labrum which are so typical for *Mormisma*.

The position of *Mormisma wygodzinskyi* Irish is not clear, as will be shown in the discussion below. For the time being, we prefer to exclude *M. wygodzinskyi* from *Namibmormisma* and consider the species generically indeterminate.

SABULEPISMA Irish gen. nov.

Type-species: *Sabulepisma multiformis* sp. nov.

Body length up to 12 mm. Body shape squat. Hypodermal pigment absent. Macrosetae in part finely plumose. Antennal sensillae flattened-campaniform (Plate 3). Head setated as in Figure 3. Distal segment of labial palp with 6-9 sensory papillae arranged in a single row. Thoracic nota with marginal setal fringes. No trichobothrial areas. Urotergites I-IX with 1+1 lateral setal fringes each. Urotergite X trapezoidal, short, with 1+1 posterolateral setal groups. Tarsal claws joined to form a single, highly sculptured structure (Plate 4), empodia lacking. Urosternites I and II with a median bristlecomb each. Urosternites III-VII with 1+1+1 bristlecombs. Urosternite VIII with 1+1 lateral bristlecombs only. Styli absent, though sometimes with indentations on coxites IX where the styli should be. Ovipositor short, conical, apices of posterior gonapophyses unsclerotised. Parameres lacking.

Distribution: Namib Desert.

Etymology: a compound of the Latin *sabulum* (sand) and *Lepisma* L.; gender feminine.

The genus is monospecific. The only other lepismatid genera with 1+1 setal fringes on the urotergites are *Mormisma* and *Namibmormisma*. *Sabulepisma* may be distinguished from both by its having plumose macrosetae. The tarsal claws are unique in the family.

Sabulepisma multiformis Irish sp. nov.

Body length of females up to 12 mm, of males up to 10 mm. Body robust, squat (fig. 2). Ground colour pale yellowish white dorsally, whitish ventrally. Hypodermal pigment absent. Scales small, tight-fitting, colourless or at most light tawny yellow dorsally, with numerous parallel striae. Macrosetae golden yellow; mostly smooth and apically rounded or bifid (fig. 6), but at least some dorsal setae finely plumose (fig. 5). The extent of plumose dorsal setae varies from a very few laterally on the thoracic nota only to almost all setae on both the thoracic nota and the urotergites.

Maxillary palp as in fig. 4, terminal segment lacking specialised sensillae. Distal segment of labial palp

bilaterally dilated, very wide, up to 3.5 times wider than long in adults of both sexes (fig. 7), narrower in nymphs; with usually eight sensory papillae arranged in a single row, but occasionally with 6, 7 or 9 papillae on one palp and eight on the other. Antennae about body length or slightly longer, with whorls of fine setae; antennal sensillae flattened-campaniform. Seta-tion of head as in generic description.

Thoracic nota with lateral and posterolateral setal fringes; macrosetae not arranged in bristlecombs, although they may be arranged in very irregular incipient bristlecomblike rows towards the anterolateral angles (fig. 9). Thoracic sterna as in figs 11, 12 and 13. Prosternum small, subtriangular, apically rounded. Meso- and metasterna widely rounded, with especially the metasternum very large. Each thoracic sternum with a narrow apical fringe of short macrosetae.

Successive posteriad pairs of legs longer, metatarsi surpassing posterior end of abdomen when legs in the normal position. Legs densely setated with long and robust macrosetae. Sexual dimorphism in setation of mesotibia; male mesotibia with a ventral brush of long robust macrosetae (fig. 10) which continues for the full length of the first tarsal segment, while the other tarsal segments each have at least one long basad macroseta which conforms to the tibial brush in length and appearance (arrowed in fig. 20); female mesotibia and -tarsus similarly with a ventral brush, but individual macrosetae of the brush about 0.6 times as long as those in similar-sized males, and spaced about twice further apart. Pretarsal claw as in generic description.

Urotergites I-IX with 1+1 lateral setal fringes each. Fringes consist of a fairly evenly spaced row of short robust and often plumose macrosetae, interspersed with irregularly spaced long slender smooth setae (figs 16, 17, 18). Specimens from the northern part of the species' range often have a group of 2-4 longer macrosetae arranged in a row on the posterolateral angle (fig. 16), at least on the antieriad urotergites, but this is lacking in most specimens from the southern part of the range. The fringe on urotergite IX is similar to that on urotergite VIII in specimens from the southern part of the range (fig. 17), but reduced in size in specimens from the northern part of the range (fig. 18). Urotergite X trapezoidal, short, width to length ratio 0.28, posteriorly emarginate, with a marginal fringe of short incurved macrosetae and slender setae; the robust macrosetae forming also 1+1 ill-defined setal groups on the posterolateral angles of the disc (fig. 19).

Urosternal setation: 1 / 1 / 1+1+1 / 1+1+1 / 1+1+1 / 1+1+1 / 1+1+1 / 1+1+1 / 1+1 / - bristlecombs. Median setal group a wide bristlecomb of up to 16 macrosetae in specimens from the southern part of the range (fig. 21), but a group of 3-4 short setae only in specimens from the northern part of the range (fig. 22). Coxites

IX subtriangular, apically rounded, with a marginal setal fringe (figs 14, 15). Styli absent in both sexes, but coxites IX of specimens from the southern part of the range retain a shallow indentation at the position where the stylus should be (fig. 8). Ovipositor short, conical, reaching to about half the length of coxite IX (fig. 15). Penis as usual for family, parameres absent (fig. 14).

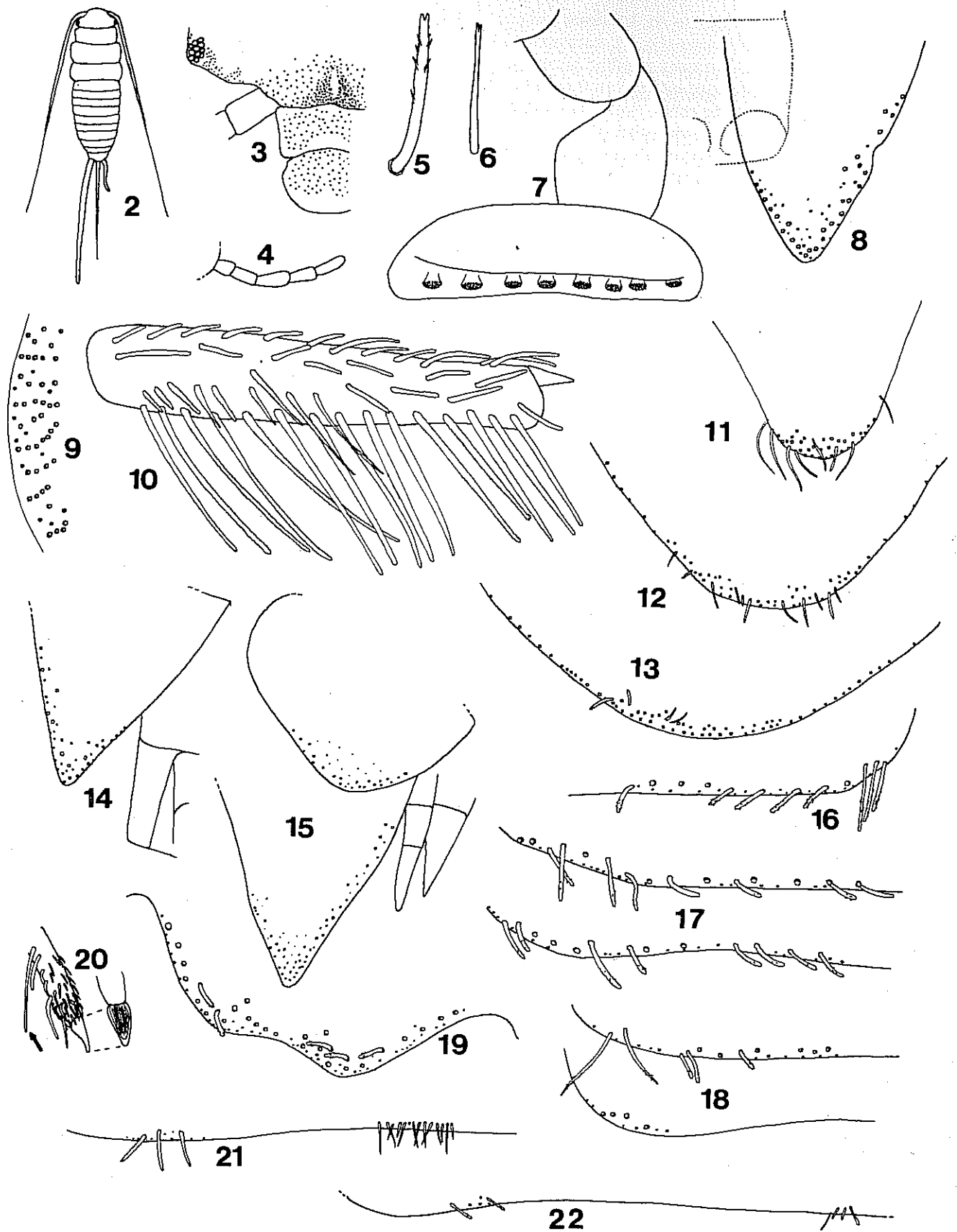
Terminal filament about half body length. Sexual dimorphism in length (see "Proportions" below) and appearance of cerci (fig. 2): About one tenth body length in females and immature males, but as long as or longer than the terminal filament in mature males. Mature males also have the cerci thick and swollen. The relatively large standard deviation for male cerci as compared to that for female cerci in the table, is the result of the fact that male cerci lengthen progressively towards maturity. Both with whorls of fine setae.

Intraspecific variation. As the specific name implies, *S. multiformis* is very variable. The intrinsic intraspecific variability is higher than normal for Lepismatidae, e.g. the extent of plumose macrosetae or the number of sensillae on the labial palp. The sexual dimorphism is also unparalleled in the family. Superimposed on all the above, the species shows marked south to north clinal variation in some characters, and three forms may be recognised, as listed below. The characterisations given for these forms should be considered indicative of trends within different populations, and not as characteristic for all individuals of that population. Many specimens are found which are intermediate between two forms with regard to one or more characters, and for most of the distribution range excepting the far north and south, at least two forms will be found to co-exist, though one or the other will usually be more common. For these reasons I refrain from according these forms subspecific status.

a) Southern form. Coxites IX indented, median urosternal bristlecomb wide, urotergite IX with full fringe, and antieriad urotergal fringes laterally undifferentiated. The common form south of the Lüderitz / Koichab area, north of which it becomes progressively replaced by the central form, although individuals conforming to the southern form may be found as far north as the Kuiseb River.

b) Central form. Coxites IX unindented, median urosternal setal groups small, urotergite IX with full fringe, and antieriad urotergal fringes laterally differentiated. Occurs throughout the main Namib dune sea, but is commoner towards its north. Specimens intermediate between this and both the previous and the next forms occur.

c) Northern form. Coxites IX unindented, median urosternal setal groups small, urotergite IX with



FIGURES 2-22: *Sabulepisma multiformis* gen. et sp. nov. 2. Body dorsal, showing appendage lengths; left cercus as in adult male, right cercus as in adult female. 3. Head. 4. Maxillary palp. 5. Macroseta of lateral mesonotum. 6. Macroseta of frons. 7. Distal labial palp, male. 8. Coxite IX, male, southern form. 9. Anterolateral mesonotum. 10. Male mesotibia. 11. Prosternum. 12. Mesosternum. 13. Metasternum. 14. Coxite IX, male, central form. 17. Urotergites VIII-IX, lateral, southern form. 18. Urotergites VIII-IX, lateral, northern form. 19. Urotergite X. 20. Tarsus and pretarsus. 21. Urosternite IV, southern form. 22. Urosternite IV, central form.

reduced fringe, and anterior urotergal fringes laterally differentiated. The common form in the Samanab area, with individuals also encountered in the Kuiseb area.

Proportions (conventions as in Irish, 1987)

		ave.	s.d.	max.	n
Body length,	female	8.35	2.85	12.00	36
Body length,	male	7.62	1.06	10.00	21
Body length,	both	8.08	1.48	12.00	57
Antennae,	female	0.98	0.14	1.33	26
Antennae,	male	0.92	0.16	1.33	15
Antennae,	both	0.96	0.15	1.33	41
Cerci,	female	0.10	0.03	0.16	28
Cerci,	male	0.51	0.17	0.82	16
Cerci,	both	0.25	0.10	0.82	44
Filum terminale,	female	0.42	0.07	0.63	26
	male	0.45	0.06	0.64	19
	both	0.43	0.06	0.64	45

Material examined:

Holotype, female, body length 8 mm, labelled: SM H 45789, 15 km S Gobabeb, 23°44'S, 15°04'E, 14-15 May 1984, J. Irish & H. Liessner. Dissected microscope preparation. SMWN type number T 004. (SMWN)

Allotype, male, body length 8 mm, same data as holotype. Dissected microscope preparation. (SMWN)

Paratypes: 105 exx.; 54 females, 29 males, 22 unsexed. All in alcohol, except as noted.

1 female, labelled: SM H 8324, 2 m W Harus Mt., LÜDERITZ, 8 May 1969, O.P.M. Prozesky. (SMWN)

5; 4 females, 1 male, labelled: SM H 5623, 10 km SW Witberg, 14 September 1971, M.-L. Penrith. (SMWN)

1 female, labelled: SM H 45800, Gobabeb, M.K. Seely, 1976, 16. (SMWN)

1 female, labelled: Hudaob dunes, M.K. Seely, 15 Oct 76, 24. (TM)

3; 2 females, 1 male, labelled: 2515Aa4, 5.1.1977, E. Holm. (TM)

6; 4 females, 2 males, labelled: SM H 45803, S.W.A. Dunes, Samanab River, 1980-11-29, Curtis. (SMWN)

1 male, labelled: Kahani dune, 13 May 1981, leg. C. Irish. (TM)

2 females, labelled: Mniszечи's Vlei, 16 October 1981, leg. Praetorius. (SMWN)

18; 9 females, 3 males, 6 unsexed, labelled: (ex SM H 45116) Kahani dune, 16 November 1981, leg. Osberg. (CZ)

1 female, labelled: Kahani dune, 16 November 1981, leg. Osberg. (TM)

3 females, labelled: SM H 45095, Kahani dune, 16 November 1981, leg. Osberg. (SMWN)

7; 4 females, 3 males, labelled: SM H 45796,

Noctivaga dune, 12 January 1982, leg. Fielden. (SMWN)

8; 6 females, 2 unsexed, labelled: SM H 45104, Noctivaga dune, 13 January 1982, leg. Fielden. (SMWN)

3; 2 females, 1 male, labelled: SM H 45799, Far East dunes, 7 February 1982, leg. Hamilton. (SMWN)

3; 2 females, 1 male, labelled: SM H 45797, Jumbo dune, 18 March 1982, leg. Praetorius. (SMWN)

2; 1 female, 1 male, labelled: SM H 45092, Kahani dune, 1 April 1982, leg. Hamilton. (SMWN)

1 female, Koichab Pan area at 2615Bcl, 4/VII/1982, leg. Univ. of Pretoria. (TM)

1 female, labelled: SM H 45802, Samanab River at 20°02'S, 13°18'E, 2-4 August 1982, M.-L. Penrith. Dissected microscope preparation. (SMWN)

1 female, labelled: SM H 45245, 10 km S Grillenthal, 4 October 1982, J. Irish. (SMWN)

5; 1 female, 3 males, 1 unsexed, labelled: SM H 45801, Uguchab River at 27°37'S, 16°10'E, 14/15 August 1983, J. Irish / Griffin. One male: dissected microscope preparation; rest in alcohol. (SMWN)

29; 6 females, 10 males, 13 unsexed, labelled as holotype. (SMWN)

3; 1 female, 2 males, labelled: W Tsondab Flats at 23°50'S, 15°04'E, 15-16 May 1984, J. Irish & H. Liessner. (SMWN)

Additional material examined: (not designated types due to damage or immaturity) 114 specimens; 1 female, 1 male, 112 unsexed. 113 (SMWN); 1 (TM)

Localities. SOUTH WEST AFRICA: Far East dunes; Gobabeb; Gobabeb, 15 km S; Grillenthal, 10 km S; Harus Mt., 2 miles W; Hudaob dunes; Jumbo dune; Kahani dune; Koichab Pan area at 2615Bc; Mniszечи's Vlei; Noctivaga dune; Samanab River at 2013Ab; Swakopmund; W Tsondab Flats at 2315Cc; Uguchab River at 2716Ca; Witberg, 10 km SW; 2515Aa.

Distribution: Dunes of the southern Namib desert. Also recorded from one locality in the northern Namib (fig. 23). Occurs on single moving barchan dune (e.g. 10 km S Grillenthal).

Etymology: from Latin *multiformis*, "having many shapes", referring to the species' variability.

SWALEPISMA Irish gen. nov.

Type-species: *Swalepisma mirabilis* sp. nov.

Body length up to 8 mm. Body spindle-shaped. Hypodermal pigment absent. Macrosetae finely plumose. Antennal sensillae scutelliform (Plate 5). Se-

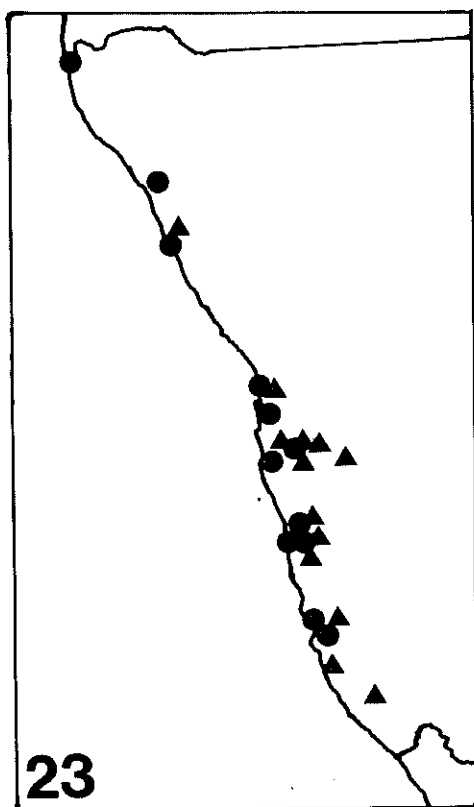


FIGURE 23: Distribution of *Sabulepisma multiformis* (triangles) and *Swalepisma mirabilis* (dots).

tation of head as in fig. 25. Distal segment of labial palp with five sensory papillae arranged in a single row. Thoracic nota with 7-9 + 7-9 lateral and 1+1 posterolateral bristlecombs. No trichobothrial areas. Urotergites I with 2+2, II-VIII with 3+3 and IX with 1+1 bristlecombs. Urotergite X subtriangular, apically rounded, with 1+1 bristlecombs. Tarsal claws normal, empodia absent (Plate 6). Urosternites I with one, II-VIII with 1+1+1 bristlecombs, of which the medians are paired. One pair of styli. Ovipositor short, apices of posterior gonapophyses minutely hyaline. Parameres lacking.

Distribution: Namib Desert.

Etymology: a compound of "SWA", an anagram for South West Africa, and *Lepisma* L.; gender feminine.

In general appearance, as well as in many important characters, *Swalepisma* resembles the more apomorph species of the subgenus *Ctenolepisma* (*Sceletolepisma*) Wygodzinsky, notably *C. pauliani* Wygodzinsky. *Swalepisma* may be distinguished from this and all other *Ctenolepisma* species by the presence of bristlecombs on urotergite IX, and by the doubled median urosternal bristlecombs.

Swalepisma mirabilis Irish sp. nov.

Body length of females up to 8 mm, of males up to 7 mm. Body spindle-shaped (fig. 24). Ground colour of

body yellowish-white. Hypodermal pigment absent. Scales dorsally transparent or at most light tawny yellowish, ventrally transparent; morphology as usual for family. Macrosetae golden yellow, finely plumose; those on frons smooth and deeply apically bifid.

Setation of head as in fig. 25. Maxillary palp slender, individual segments short, with a scoop-shaped apical sensilla (fig. 27). Distal segment of labial palp feebly bilaterally dilated, about as wide as long, with five (occasionally four) sensory papillae arranged in a single row (fig. 26). Eye smallish, black, composed of about 11 ommatidia. Antennae with whorls of fine setae, sensillae as for genus.

Nape setated. Pro- and metanota with 7+7, mesonotum with 9+9 lateral bristlecombs of 2-6 macrosetae each. Each thoracic notum also with 1+1 very laterally situated posterolateral bristlecombs of 3 macrosetae each (fig. 31).

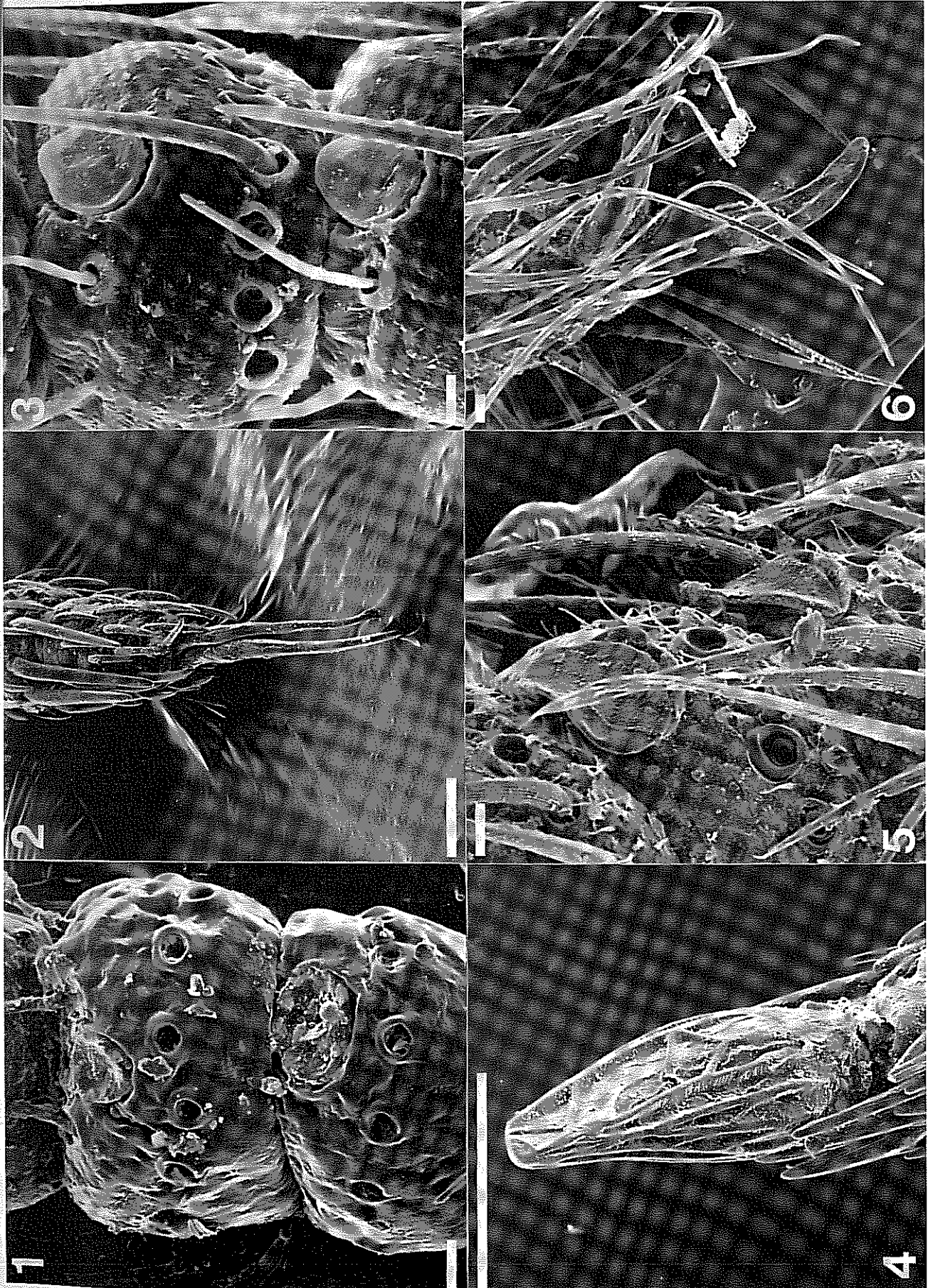
Urotergal setation: 2+2 / 3+3 / 3+3 / 3+3 / 3+3 / 3+3 / 3+3 / 3+3 / 1+1 / 1+1 bristlecombs. Submedian and lateral bristlecombs usually of 2, occasionally 3, macrosetae each. Sublateral bristlecombs of 3-5 macrosetae each (fig. 38). Urotergite X subtriangular, short, width to length ratio 0.36, posteriorly rounded, with 1+1 small bristlecombs of 2-3 macrosetae each (fig. 33).

Thoracic sterna shaped as in figs. 28, 29, 30; with a narrow posterior marginal setal fringe, and an anteromedian setal tuft each. Legs lengthening posteriorwards. Tibia III about twice longer than tibia I. Tibiae and apical femora robustly setated. Tarsus with a distinctive setal tuft (fig. 32); with two claws, but lacking an empodium.

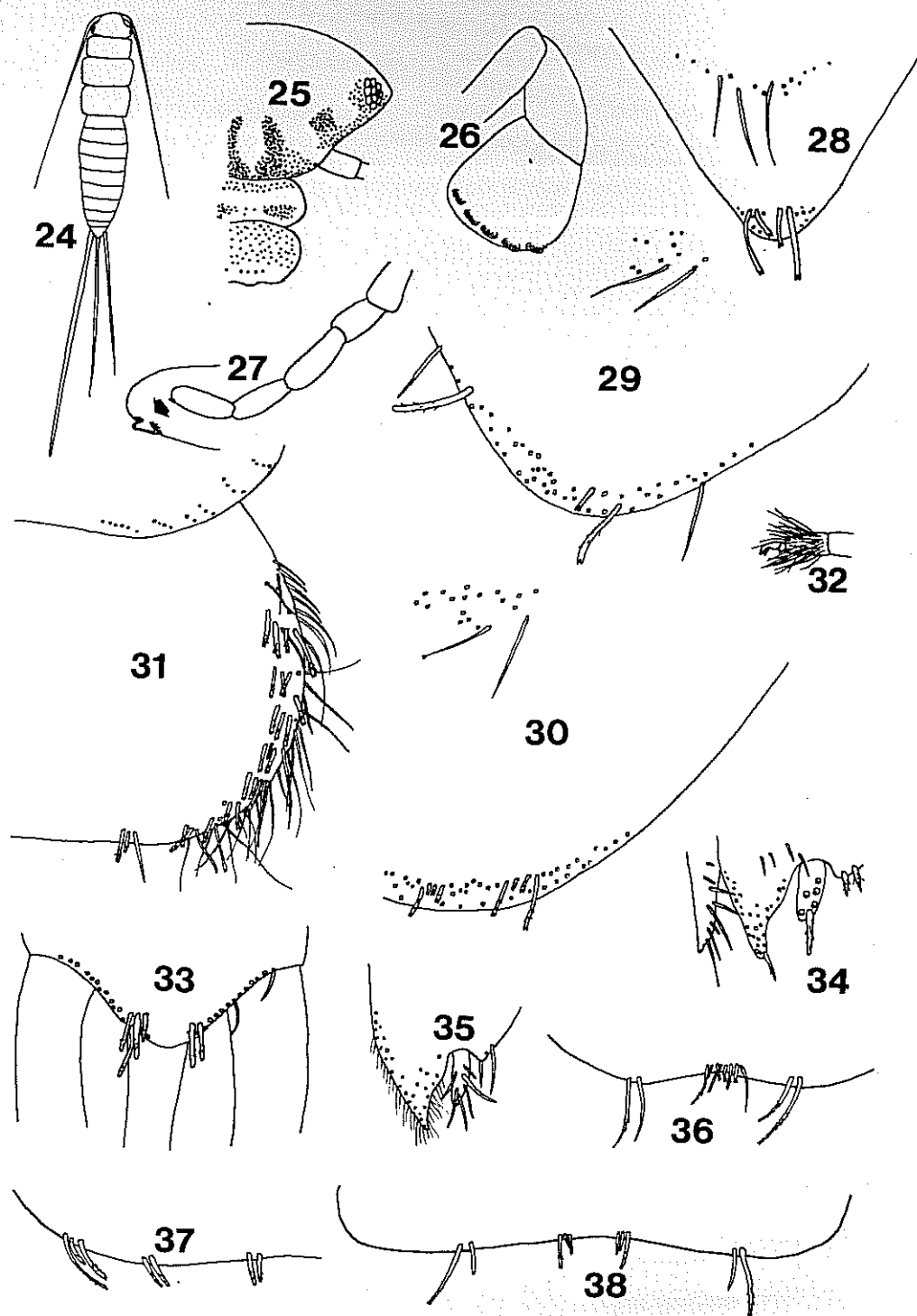
Urosternal setation: 1 / 1+(1+1)+1 / 1+(1+1)+1 / 1+(1+1)+1 / 1+(1+1)+1 / 1+(1+1)+1 / 1+(1+1)+1 / 1+(1+1)+1 / 1+1+1 (male) of 1+1 (female / - bristlecombs. Median bristlecombs each consisting of two smaller, separate bristlecombs of a total of 5-8 macrosetae (fig. 37), which may be confluent on the posteriad urosternites (fig. 36). Lateral bristlecombs of 2, occasionally only 1, macrosetae each. Inner processes of coxites IX subtriangular, with a wide marginal setal fringe (figs. 34, 35). Both sexes with one pair of very short, atrophied styli only, which attain about two-thirds the length of the inner process of coxites IX.

Ovipositor short, conical, not reaching to the apices of coxites IX, tips of gonapophyses acute, faintly hyaline (fig. 34). Penis as usual for family, parameres absent.

Caudal filaments setated with whorls of setae. Terminal filament unmodified, of normal length. Sexual dimorphism in length (see "Proportions" below) and appearance of cerci (fig. 24): females and immature males with cerci normal and just shorter than terminal



PLATES 1-6. Antennal sensillae and pretarsi of Lepismatidae species. Scale bars: 1 micron each. 1. *Namibmormisma muricaudata*. Distal antennal segments with sensillae. 2. *Namibmormisma muricaudata*. Pretarsus. 3. *Sabulepisma multififormis*. Distal antennal segments with sensillae. 4. *Sabulepisma multififormis*. Pretarsus. 5. *Swalepisma mirabilis*. Distal antennal segments, with sensillae. 6. *Swalepisma mirabilis*. Pretarsus.



FIGURES 24-38: *Swalepisma mirbilis* gen. et sp. nov. 24. Body, dorsal, showing appendage lengths; left cercus as in male, right cercus as in female. 25. Head. 26. Distal labial palp. 27. Maxillary palp. 28. Prosternum. 29. Mesosternum. 30. Metasternum. 31. Posterolateral mesonotum and lateral metanotum. 32. Distal tarsus. 33. Urotergite X, male. 34. Female genital area. 35. Coxite IX, male. 36. Urosternite VIII, male. 37. Urotergite VI. 38. Urotergite V, lateral.

filament, adult males with cerci fleshy, swollen and usually longer than terminal filament.

Proportions

		ave.	s.d.	max.	n
Body length,	female	6.55	0.78	8.25	24
Body length,	male	6.23	0.57	7.00	16
Body length,	both	6.43	0.69	8.25	40
Antennae,	female	0.64	0.09	0.82	11
Antennae,	male	0.65	0.09	0.80	8
Antennae,	both	0.64	0.09	0.82	19
Cerci,	female	0.51	0.07	0.63	16
Cerci,	male	0.70	0.11	1.00	15
Cerci,	both	0.61	0.09	1.00	31
Filum terminale,	female	0.60	0.05	0.67	18
	male	0.53	0.07	0.70	16
	both	0.56	0.06	0.70	34

Material examined:

Holotype, female: body length 8.25 mm, labelled; SM H 5623, 10 km SW Witberg, Lüderitz, 14 Sept. 1971, CGC, M.J. + M.-L.P. In alcohol. SMWN type-number T 013. (SMWN)

Allotype, male: body length 6.25 mm, labelled: SM H 7027, Hoanib R at 19°23'S, 13°05'E, 8 December 1971, MJP. In alcohol. (SMWN)

Paratypes: 61 specimens; 23 females, 22 males, 16 unsexed. All in alcohol, except as noted.

3 males, labelled: Natab, 29 November 1975, M.K. Seely. (TM)

2; 1 female, 1 male, labelled: 30 km N Lüderitz, 5 October 1979, Holm & Scholtz. (TM)

1 female, labelled: Torra Bay, 20 November 1980, B.A. Curtis. (SMWN)

1 male, labelled: Noctivaga dune, 12 August 1981, leg. Osberg. (SMWN)

1 female, labelled: Dunes S Swakopmund, 12 December 1981, J. Irish. (SMWN)

6; 2 females, 2 males, 2 unsexed, labelled: Rooibank, 18 December 1981, leg. Praetorius. (SMWN)

1 female, labelled: Noctivaga dune, 13 January 1982, leg. Fielden. (SMWN)

15; 7 females, 7 males, 1 unsexed, labelled: Northern Namib at 17°19'S, 11°50'E, 27/28 January 1982, J. Irish. (SMWN)

4; 3 females, 1 male, labelled: 3 km E Bosluisbaai, 31 January - 2 February 1982, J. Irish. (SMWN)

1 female, labelled: Rooibank, 9 February 1982, leg. Hamilton. (SMWN)

1 male, labelled: SM H 45167, 2 km N Sylvia Hill, 22/23 June 1982, J. Irish. (SMWN)

1 male, labelled: Diamond Area 2 at 25°02'S, 15°12'E, 25/26 June 1982, J. Irish. (SMWN)

2; 1 female, 1 unsexed, labelled: Grasplatz, 2 km N, 6 October 1982, J. Irish (SMWN)

1 male, labelled: 3 km E Haris, 6 October 1982, J. Irish. Dissected microscope preparation. (SMWN)

21; 5 females, 4 males, 12 unsexed, labelled: Diamond Area 2 at 23°59'S, 14°39'E, 16/17 May 1984, J. Irish / H. Liessner. (CZ)

Additional material: (not designated types due to damage or immaturity) 22 specimens; 11 females, 2 males, 9 unsexed. 20 (SMWN); 2 (TM)

Localities. SOUTH WEST AFRICA: Bosluisbaai, 3 km E; Conception; Diamond Area 2 at 2314Dc; Diamond Area 2 at 2515Aa; Grasplatz, 2 km N; Haris, 3 km E; Hoanib R at 1913Ac; Kahani dune; Koichab Pan Area at 2615Bc; Lüderitz, 30 km N; Natab; Noctivaga dune; Northern Namib at 1711Bd; Rooibank; Sandwich Harbour; Swakopmund, dunes S; Sylvia Hill, 2 km N; Torra Bay; Uniab River, dunes in; Witberg, 10 km SW.

Distribution. Dune seas of the Namib Desert, from Lüderitz to the Kunene River, usually near the coast (fig. 23). Occurs on single barchan dunes (e.g. 3 km E Haris).

Etymology: from Latin *mirabilis*, "extraordinary, unusual".

DISCUSSION

The three genera treated here are evidently closely related. They share synapomorphic characters such as the setation of the head, modifications of the tarsi, reduction or loss of styli, and modifications of the caudal filaments.

The most plesiomorphic member within this group, *Swalepisma mirabilis*, shares many characters with *Ctenolepisma pauliani*, such as similar tarsal claws (lacking empodia), bilaterally dilated distal segment of the labial palp, a subtriangular tenth urotergite, similar tibial setation, presence of a median bristlecomb on the male urosternite VIII, unusual proportions of the caudal filaments, and similar habits. It clearly differs from *Ctenolepisma* in the characters noted in the generic description. It seems probable that *Swalepisma* evolved from a *C. pauliani*-like ancestor. *Sabulepisma* shares many characters with both *Swalepisma* and *C. pauliani*. It probably evolved from ancestral *Swalepisma*-like stock before the latter acquired its distinctive antennal sensillae. *Sabulepisma* subsequently acquired its unique tarsal claws and lost its styli. Since loss of styli is an apomorphic trait in Lepismatidae, it follows that *S. multiformis*, which retains indented coxites IX in its southern form, had a southern origin. This is normal for most ultrapsammophilous Namib taxa (Irish, 1986a) and we may assume the same for *S. mirabilis*. Figure 23 shows that

Swalepisma usually occurs nearer to the coast than *Sabulepisma*. Accepting the monophyly of these two taxa as proposed above, this probably means that they evolved in response to the dissimilar conditions in coastal as opposed to inland dunes. A similar situation was noted for the ultrapsammophilous *Comicus calcaris* Irish and *C. arenarius* Ramme (Orthoptera: Schizodactylidae) by Irish (1986a). In the latter work the differences between coastal and inland dunes was also considered to be the reason for the absence of many common southern Namib taxa from the northern Namib. In the present cases we again see the coastal southern Namib *S. mirabilis* to be common in the northern Namib dunes, while the interior southern Namib *S. multiformis* is known from the northern Namib from but a single locality. It is significant that the latter (Samanab River) is on the inland side of the narrow subcoastal dune strip, while the nearest record for *S. mirabilis* (Torra Bay) is on the seaward side of the same strip of dunes. It would be interesting to see whether this is also the case elsewhere in the northern Namib.

The difficult position of *Mormisma wygodzinskyi* was noted above. It resembles the *Namibmormisma* species in its antennal sensillae, setation of the head, labial palpi and tarsal claws. On the other hand it shares many characters with *Sabulepisma multiformis*, notably its long antennae, sexually dimorph cerci and urotergal setation. Even more enigmatic, its urosternal setation resembles that of *Swalepisma mirabilis*. In habitat preference it also resembles *Sabulepisma* and *Swalepisma*, both these being predominantly slipface dwellers, while *Namibmormisma* are hummock dwellers. The two *Namibmormisma* species themselves are closely related, and are the most apomorphic (modified cerci, shortened antennae etc.) of the taxa here considered, but beyond this their position in the overall phylogeny is not clear. It is expected that a forthcoming revision of the Namib "*Hyperlepisma*" species, which resemble *Namibmormisma* and are also hummock dwellers, will throw more light on the matter.

However, the fact that *Namibmormisma* belongs to the present group of taxa is in no dispute, nor is the fact that it evolved from endemic Namib taxa in the Namib. It is therefore historically unrelated to the Saharan *Mormisma*, and their similarities, including the poculiform antennal sensillae, must be regarded as the products of parallel evolution in response to similar

environments and habits. It is probable that *Mormisma* as well as the Saharan *Hyperlepisma* species also evolved from *Ctenolepisma*-like stock, and the absence of median bristlecombs on urosternite VII in *Mormisma* and one of the two Saharan *Hyperlepisma* species seems to confirm this. Most Saharan *Ctenolepisma* species belong to the species groups *villosa* and *michaelseni*, which lack median bristlecombs on urosternite VII. The southern African *Ctenolepisma* species (species group *grandipalpis* and others), from which the Namib taxa and ultimately *Namibmormisma* are probably derived, with few exceptions all have such bristlecombs (Irish, 1987).

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